

Contributions of gopher mound and casting disturbances to plant community structure in a Cascade Range meadow complex

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Abstract: Pocket gophers (Geomyidae) are major agents of disturbance in North American grasslands. Gopher mounds bury existing plants and influence community structure through various mechanisms. However, in mountain meadows that experience winter snowpack, gophers also create winter castings, smaller tube-shaped deposits, previously ignored in studies of plant–gopher disturbance relationships. We studied the influences of the Mazama pocket gopher (*Thomomys mazama* Merriam, 1897) in montane meadows of the Oregon Cascades, quantifying community patterns at larger spatial scales than previously studied in this system and considering, for the first time, effects of both mounds and castings. We measured cover of disturbance and individual plant species along twenty 5 m transects in each of four plots with differing species composition. Total plant cover was negatively correlated with mounds and castings. However, only mounds influenced growth-form dominance, reducing graminoid cover and increasing the forb–graminoid ratio — effects attributable to the greater volume and longevity of mounds. Forb–disturbance relationships were variable among plots, likely due to differences in species' tolerance of burial. Transect-scale richness and heterogeneity (variation in composition within transects) increased with disturbance. We conclude that frequent, small-scale disturbances create a shifting mosaic of vegetation states, reducing graminoid dominance and enhancing species richness and heterogeneity at larger spatial scales.

Key words: gopher disturbance, mounds, castings, meadow community structure.

Résumé : Les gaufres (Geomyidae) constituent des agents majeurs de perturbation dans les prairies nord-américaines. Les gaufres enterrent dans les monticules des plantes existantes et influencent la structure de leurs communautés. Cependant, dans les prairies de montagnes soumises à des accumulations de neige, les gaufres déposent également des moules hivernaux, sous forme de dépôts plus petits en forme de tube, que l'on a ignorés dans les études sur la relation de perturbation plante–gaufre. Les auteurs ont étudié l'influence du gaufre de Mazama (*Thomomys mazama* Merriam, 1897) dans les prairies de montagnes de la région des Cascades en Oregon, en quantifiant les patrons des communautés à une échelle spatiale plus large que les études précédentes dans ce système, considérant pour la première fois les effets combinés des monticules et des moules. Ils ont mesuré la couverture de perturbation et les espèces de plantes individuelles le long de 20 transects de 5 m, dans chacune de quatre parcelles ayant des compositions en espèces différentes. On observe une corrélation négative entre la couverture totale des plantes et celle des monticules et des moules. Cependant, seuls les monticules influencent la dominance d'une forme de développement, avec une réduction de la couverture en graminoides et une augmentation du rapport non-graminoides–graminoides, effets attribuables au plus fort volume et la plus grande longévité des monticules. Les relations entre non-graminoides et perturbations varient entre les parcelles, dû vraisemblablement aux différences de la tolérance à l'enterrement des espèces. La richesse à l'échelle des transects et l'hétérogénéité (variation de la composition dans les transects) augmente avec la perturbation. Les auteurs concluent que des perturbations fréquentes et à petite échelle créent une mosaïque mobile de stades de végétation, réduisant la dominance des graminoides et augmentant la richesse en espèces ainsi que l'hétérogénéité aux plus grandes échelles spatiales. [Traduit par la Rédaction]

Mots-clés : perturbation par les gaufres, monticules, moules, structure des communautés.

Introduction

Physical disturbances caused by pocket gophers (Geomyidae) are among the most frequent and widespread forms of disturbance in North American grasslands. As they excavate subterranean burrows, gophers deposit soil in mounds that bury existing vegetation. Mounds can occupy up to 25%–30% of the ground surface in a given year (Huntly and Reichman 1994). Mounding disturbance can play a key role in the community structure of grasslands (Reichman 2007), reinitiating succession at a local scale and altering species composition by promoting growth forms adapted to disturbance. Although these relationships have been well documented in lowland prairies, they have received limited attention in higher-elevation (montane or subalpine) systems,

where responses to disturbance may differ due to a shorter growing season, dominance by perennial, often clonal species (Sherrod et al. 2005; Jones et al. 2008), and other factors. In addition, in mountain grasslands, presence of a winter snowpack contributes to the formation of gopher castings — soils that are packed into winter tunnels at or above the ground surface and are exposed or settle after snowmelt (Reichman 2007; Knight 2009) (Fig. 1a). In contrast to mounds, castings are linear in form, result in shallower burial, and are deposited when plants are dormant. Similar to mounds, however, they can cover large portions of the ground surface. Although the physical characteristics of winter castings and associated geomorphic processes have been described (Thorn 1978; Reichman 2007; Knight 2009), to our knowledge, the

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Fig. 1. Examples of gopher disturbances: (a) castings exposed at the time of snowmelt, and (b) old mounds (note weathering and stones), a fresh mound, and an associated hole (center).



influences of castings on plant community structure have not been examined.

Previous studies, conducted primarily in lowland systems, demonstrate that mounds can influence plant communities in a variety of ways. For example, mounds can provide establishment sites for annuals in communities dominated by perennials (Foster and Stubbendieck 1980; Schaal and Leverich 1982; Tilman 1983) or can favor survival of forbs relative to graminoids (grasses and sedges) (Mielke 1977; Foster and Stubbendieck 1980; Martinsen et al. 1990; Sherrod et al. 2005). Mounding can also affect species diversity. In some systems, successional changes on mounds are consistent with the intermediate disturbance hypothesis (IDH; Grime 1973; Connell 1978), with species richness peaking on intermediate-aged mounds (Williams et al. 1986; Collins 1989; Reader and Buck 1991). In other systems, species accumulate continuously over time (Rogers et al. 2001; Sherrod et al. 2005; Jones et al. 2008).

Gopher disturbances are patchy in space and time, creating a “spatiotemporal mosaic” of vegetation states (sensu Levin 1992) that affects community structure at larger spatial scales. By creating habitat variation at smaller scales, mounding can increase beta diversity or the spatial heterogeneity of species composition at larger scales (Gibson 1989; Seabloom et al. 2005). The presence of mounds can also enhance gamma or “landscape-scale” diversity by allowing early- and late-successional species to coexist in the

same grassland (Tilman 1983; Hobbs and Mooney 1985; Inouye et al. 1987; Gibson 1989).

In this study, we explore relationships between plant community structure and gopher disturbance in high-elevation meadows of the Oregon Cascade Range. We build on an earlier study of this system (Jones et al. 2008), based on a chronosequence of mounds, that demonstrated increasing plant cover and richness (but not evenness) as mounds age, reduced dominance by graminoids (increased ratio of forb to graminoid cover) on mounds relative to adjacent undisturbed meadow, and greater heterogeneity of species composition among mounds than among similar-sized patches of undisturbed meadow. Here, we examine whether similar relationships exist at larger spatial scales — encompassing broader areas of disturbed and undisturbed meadow — and how these relate to the individual and combined effects of castings and mounds. We hypothesized that patterns observed at the scale of mounds (Jones et al. 2008) would extend to this larger spatial scale. Specifically, we hypothesized that increasing disturbance (greater cover of mounds plus castings) would lead to lower plant cover, reduced dominance by graminoids, reduced richness (or, alternatively, a hump-shaped pattern), no change in evenness, and increased heterogeneity of species composition. We also hypothesized that both mounds and castings would contribute to these relationships, but less often for castings, due to their smaller volume and more transient nature.

Methods

Study site

The study area, Bunchgrass Ridge, is a broad, raised plateau at an elevation of ~1220–1375 m in the Oregon Cascade Range (44°17'N, 121°57'W). Slopes are gentle (<5%) and generally face south to southwest. Bunchgrass Ridge supports a mosaic of dry montane meadows and forests of varying age, resulting from two centuries of conifer encroachment (Halpern et al. 2010; Rice et al. 2012). Meadows are dominated by graminoids (e.g., *Carex pensylvanica*, *Festuca idahoensis*) and perennial forbs (e.g., *Phlox diffusa*, *Lupinus latifolius*, *Cirsium callilepis*, *Achillea millefolium*) (Halpern et al. 2012) typical of high-elevation plateaus and south-facing slopes in the central Cascades (Halpern et al. 1984). Disturbance attributed to the Mazama pocket gopher (*Thomomys mazama* Merriam, 1897) is common in these meadows (Jones et al. 2008).

Meadow soils are Vitric Melanocryands, deep (>170 cm) fine to very fine sandy loams derived from andesitic basalt and volcanic ash deposits (D.A. Lammers, personal communication, 2005). The climate is characterized by warm, dry summers and cool, wet winters, with deep accumulations of snow that can persist into May or June. Average annual temperatures at Santiam Pass (17 km to the north, 1488 m elevation) range from 0.7 °C (maximum) and –6.9 °C (minimum) in January to 22.8 °C (maximum) and 6.1 °C (minimum) in July. Average annual rainfall is 216.5 cm; <8% of this falls during the summer months. Snowpack at Santiam Pass peaks in March at an average depth of 2.6 m (data from 1948–1985, Western Regional Climate Center <http://www.wrcc.dri.edu/cgibin/cliMAIN.pl?orsant> [accessed 20 February 2012]).

Sampling design and measurements

We established a total of four 5 m × 20 m plots in three spatially segregated meadows. We chose the general locations and orientations of plots subjectively, to lie distant from forest edges, to represent distinctly different meadow communities, and to sample areas with moderate but variable disturbance within each plot. At each location, a blind toss of a chaining pin was used to establish one corner of the plot; the remaining corners were then surveyed to within 1% of the expected perimeter.

Each plot comprised twenty 5 m transects spaced at 1 m intervals; each transect was sampled with 25 contiguous quadrats (20 cm × 20 cm). Within each quadrat, we estimated cover (%) of

soil disturbance and individual plant species (values <1% were estimated as 0.5% or 0.1%, values of 1%–10% to the nearest 1%, and values >10% to the nearest 5%). Disturbance was sampled between 20 and 30 June 2011, soon after snowmelt and prior to emergence of most plants, when mounds and castings were most visible. Disturbance types included fresh mounds, old mounds, castings, surface tunnels, and holes. Fresh mounds, created during the current growing season, consisted of loose, uncompacted soil with no vegetation cover (Fig. 1b). All other mounds, defined as “old,” were characterized by some degree of compaction or weathering; most had some plant cover. Castings, the remnants of snow tunnels into which soil had been deposited during winter, were ~6–10 cm in diameter and often extended in sinuous or dendritic forms for a metre or more (Fig. 1a). Castings could occur on or adjacent to mounds but were easily distinguished by their linear form and high concentration of leaf fragments. We also estimated cover of surface tunnels (concave or hemispherical tunnels at the ground surface) and holes (openings to subterranean tunnels; Fig. 1b); however, these were uncommon.

Vegetation was sampled independently of soil disturbance, between 7 July and 12 August 2011. One exception was *Claytonia lanceolata*, a spring ephemeral, which was sampled coincidentally with ground disturbance. We estimated cover of each plant species as the vertical projection into each quadrat. We identified all plants to species, but treated *Fragaria vesca* and *F. virginiana* as a single taxon. Nomenclature follows Hitchcock and Cronquist (1973). Fresh mounds or holes that appeared to be new at the time of vegetation sampling were noted, but were rare.

Data manipulation and analyses

Quadrat data were summarized at the transect scale. Measures of disturbance included mean cover of old mounds, castings, and their summation (total disturbance). Plant community attributes included the following: mean total cover of plants, forbs, and graminoids; ratio of forb to graminoid cover; species richness (number of species per transect); and evenness (the equitability of abundance among species). Evenness was computed as the modified form of Hill's ratio $(N_2 - 1)/(N_1 - 1)$ (Hill 1973; Alatalo 1981). N_2 is the reciprocal of Simpson's index $(1/\sum p_i^2)$ and N_1 is the exponent of Shannon's information measure, $\exp(-\sum p_i \cdot \ln p_i)$, where p_i is the proportional abundance (cover) of species i . N_1 and N_2 were computed in the vegan package (Oksanen et al. 2011). Finally, we calculated an index of heterogeneity (variation in species composition) as the mean Bray–Curtis dissimilarity (Bray and Curtis 1957) among all pairs of quadrats within a transect, using the ecodist package (Goslee and Urban 2007).

To assess the hypothesized relationships between disturbance and plant community attributes, we used linear mixed-effects models (lme4 package; Bates et al. 2011). Disturbance variables were treated as fixed effects, and plot was treated as a random effect to account for potential correlation of errors within plots. Each model used the maximal random-effects structure justified by the data; i.e., either a random intercept or a random intercept and random slope where this significantly improved model fit (Zuur et al. 2009). For fixed effects (disturbance variables), p values were obtained with the pamer.fnc() function (LMERConvenience-Functions package; Tremblay 2011), which computes upper- and lower-bounded p values for the analysis of variance (ANOVA) for each fixed effect according to the range of possible degrees of freedom (df). These values generally differed by <0.001; thus, for simplicity, we report the more conservative upper-bounded p and the corresponding df. In addition to the linear model, we modeled richness as a quadratic function to test whether its relationship with disturbance conformed to the IDH (peaking at intermediate disturbance). We compared quadratic and linear models by using a likelihood-ratio test.

Finally, to assess the contributions of old mounds and castings to the overall relationships with disturbance, we modeled each

community attribute as a function of the cover of old mounds and castings, treating the latter as additive fixed effects, with plot as a random effect (as above). We used the R statistical package (R Development Core Team 2011) for all analyses.

Results

Frequency and cover of disturbance types

Old mounds and castings were the most common types of gopher disturbance. Roughly 60%–70% of quadrats contained some form of disturbance. Among plots, cover of old mounds averaged 12%–21%, castings 9%–14%, and total disturbance 25%–33%, with castings contributing 30%–50% of total gopher disturbance. Tunnels and holes occurred in <5% of quadrats and fresh mounds in <0.2% of quadrats.

Floristics and variation in species composition among plots

We observed a total of 33 taxa, including 22 forbs, 10 graminoids, and one shrub (a seedling) (Table 1). Among plots, total species richness ranged from 21 to 27. Graminoid richness was similar among plots (8–9 species), but forb richness varied (13–18 species). Species composition also varied among plots, with some species abundant in one or two plots, but absent or rare in the others. For example, *Phlox diffusa* was very abundant in plots 2 and 3, relatively infrequent in plot 1, and absent from plot 4. Most (70%) of the graminoid species occurred in all plots (albeit at varying cover), but 20% were found in only one plot. Among the forb species, 41% were found in all plots, but 32% were found in only one plot (Table 1).

Plant community relationships with total, mound, and casting disturbance

As predicted, total plant cover declined significantly with total disturbance (cover of mounds plus castings; random-intercept model; Fig. 2a). However, due to variation among plots, there was no significant relationship with total disturbance for forb or graminoid cover, or their ratio (random-slope models; Figs. 2b–2d). Counter to expectation, species richness (number of species per transect) increased significantly with total disturbance (random-intercept model; Fig. 3a). The increase amounted to an average of one species for each increase in disturbance of 20 percentage points. The attempt to model richness as a quadratic function, to test consistency with the IDH, did not yield a better fit than the linear model ($\chi^2 = 0.237$, $df = 1$, $p = 0.63$). As predicted, species evenness was unrelated to total disturbance (Fig. 3b), and heterogeneity (average pairwise dissimilarity of quadrats) was positively related, although slopes differed among plots (random-slope model; Fig. 3c).

As predicted, cover of both mounds and castings contributed to declines in total plant cover (Table 2). However, only mounds contributed to the decline in graminoids and to increases in forb–graminoid ratio and heterogeneity. Counter to expectation, species richness was positively correlated with cover of castings, but only marginally so ($p = 0.098$) with mounds.

Discussion

The two primary goals of this study were (i) to explore relationships between plant community structure and gopher disturbance at spatial scales much larger than those of previous mound-based studies of this system (Jones et al. 2008), and (ii) to assess the contributions of both mounds and castings to these relationships. At Bunchgrass Ridge, castings were a common form of disturbance, occupying ~10% of the ground surface and contributing roughly 30%–50% of all gopher disturbance. Given the ubiquity but smaller size of castings, we hypothesized similar, albeit less often significant, effects compared with mounds. Indeed, total plant cover was negatively correlated with cover of both mounds and castings, demonstrating the importance of castings as a form

Table 1. Species' frequency of occurrence ($n = 500$ quadrats·plot⁻¹) and mean cover among plots.

Species	Plot 1		Plot 2		Plot 3		Plot 4	
	Freq (%)	Cover (%)	Freq (%)	Cover (%)	Freq (%)	Cover (%)	Freq (%)	Cover (%)
Forbs								
<i>Phlox diffusa</i>	35.8	6.2	97.0	27.6	81.0	35.8		
<i>Lupinus latifolius</i>	91.2	15.2	87.2	17.2	66.0	8.6	89.6	16.6
<i>Hieracium scouleri</i>	2.0	0.1	2.6	0.4	16.8	1.5	79.4	10.4
<i>Achillea millefolium</i>	64.6	4.2	57.6	4.3	5.2	0.3	35.6	2.1
<i>Arenaria macrophylla</i>	84.4	3.8	92.0	4.6	16.8	0.5		
<i>Orthocarpus imbricatus</i>	11.4	0.3	88.4	7.2	25.8	0.7		
<i>Cirsium callilepes</i>	53.8	5.7	14.4	0.9			10.6	0.6
<i>Fragaria</i> spp.							63.8	7.0
<i>Erigeron aliciae</i>	19.8	3.3	20.2	2.8	2.2	0.2	2.0	0.2
<i>Aster radulinus</i>							34.4	4.8
<i>Iris chrysophylla</i>	2.4	0.2	0.4	<0.1	3.8	0.3	41.4	3.1
<i>Claytonia lanceolata</i>	27.4	0.5	28.6	0.5	75.6	1.8	1.8	<0.1
<i>Penstemon procerus</i>			6.0	0.8				
<i>Comandra umbellata</i>			16.2	0.6			6.2	0.2
<i>Calochortus subalpinus</i>	19.2	0.3	16.0	0.2	6.0	0.1	1.2	<0.1
<i>Aster ledophyllus</i>			4.2	0.5				
<i>Viola nuttallii</i>	3.6	0.1	8.8	0.2	4.4	0.1	4.8	0.1
<i>Agoseris aurantiaca</i>	4.6	0.2	3.4	0.1	5.0	0.2	0.4	<0.1
<i>Lilium columbianum</i>	2.6	0.1						
<i>Lomatium triternatum</i>	1.6	<0.1	1.2	<0.1	2.0	<0.1		
<i>Rumex acetosella</i>							1.8	<0.1
<i>Fritillaria lanceolata</i>			0.6	<0.1				
Graminoids								
<i>Carex pensylvanica</i>	99.6	20.0	93.2	7.3	99.2	10.2	99.6	12.8
<i>Festuca idahoensis</i>	86.8	5.8	85.6	6.8	70.8	8.7	97.0	15.4
<i>Bromus carinatus</i>	67.0	4.1	29.0	0.7	26.8	1.7	71.4	2.7
<i>Danthonia intermedia</i>	11.0	0.2	31.0	0.6	46.8	1.4	52.6	1.0
<i>Elymus glaucus</i>	42.2	2.0	23.0	0.4	4.6	0.1	11.6	0.4
<i>Stipa occidentalis</i>	7.0	0.6	4.6	0.3	18.8	1.0	1.6	0.1
<i>Agropyron repens</i>			1.6	<0.1	5.2	0.2	8.2	0.2
<i>Poa pratensis</i>	2.2	<0.1	6.4	0.1	1.6	0.1	1.8	<0.1
<i>Festuca viridula</i>	0.8	<0.1						
<i>Luzula campestris</i>			0.2	<0.1				
Shrubs								
<i>Acer circinatum</i>							0.1	<0.1
	Plot 1		Plot 2		Plot 3		Plot 4	
No. of forb species	15		18		13		14	
No. of graminoid species	8		9		8		8	
Total no. of species	23		27		21		23	

Note: Species are listed by descending abundance (cover) within each growth form.

of disturbance. However, relationships with growth-form dominance, diversity, and heterogeneity present a more complex picture — one in which the effects of mounds and castings not only differ, but vary with context (i.e., the location or community characteristics of plots).

The relative abundance of forbs and graminoids

We hypothesized that increasing disturbance would benefit forbs over graminoids, as demonstrated in other grasslands (Mielke 1977; Foster and Stubbendieck 1980; Martinsen et al. 1990; Sherrod et al. 2005) and in the mound-based study of this system (Jones et al. 2008). Relationships with total disturbance were equivocal, with no consistent trends among plots in the cover of forbs, graminoids, or their ratio. However, when only mound disturbance was considered (as in previous studies), trends were consistent with expectation: forbs benefited from disturbance relative to graminoids, with declines in graminoids driving this trend. Castings, meanwhile, did not have a consistent effect on graminoids or on the forb–graminoid ratio. These results suggest that when the forms of gopher disturbance are not distinguished, neutral or variable effects of castings can mask the strong negative relationship between mounds and graminoids. Forbs, on the other hand, showed inconsistent responses to both mounds and

castings. These complexities lead to two basic questions: why might castings and mounds differ in their effects on vegetation, and why might relationships between growth forms and disturbance vary among plots?

Castings and mounds differ in several important ways that are likely to influence vegetation. First, they differ in size and density: mounds are typically taller (5–25 cm) and broader (20–50 cm) than castings (6–10 cm in diameter) (Reichman 2007) and appear to contain considerably less organic matter. Second, they differ in longevity: castings are assimilated into the meadow matrix relatively quickly — likely within a growing season — whereas mounds decay gradually over several years (Reichman 2007). The greater depth and longevity of burial by mounds can have a discriminating effect on plant reemergence (Antos and Zobel 1985; Dong et al. 2011), the principal means by which mounds are recolonized in these high-elevation environments (Sherrod et al. 2005; Jones et al. 2008). Excavations of root systems from mounds at Bunchgrass Ridge (M.F. Case, unpublished data) indicate that most forb species are able to reemerge from burial. New shoots and associated roots were commonly connected to old root systems 5–10 cm below the surface of a mound (just below the former ground surface). Although in some systems graminoids can

Fig. 2. Relationships between total disturbance (cover of mounds plus castings) and plant cover. Points represent mean transect values ($n = 20$ per plot). (a) Total plant cover ($\beta = -0.48763$, $SE(\beta) = 0.6656$, $F = 53.68$, $df = 74$, $p < 0.001$). (b) Forb cover ($\beta = -0.2120$, $SE(\beta) = 0.2447$, $d^2 = 0.2070$, $F = 0.725$, $df = 70$, $p = 0.3976$). (c) Graminoid cover ($\beta = -0.2654$, $SE(\beta) = 0.1869$, $d^2 = 0.1228$, $F = 1.98$, $df = 70$, $p = 0.1637$). (d) Ratio of forb to graminoid cover ($\beta = -0.01274$, $SE(\beta) = 0.03316$, $d^2 = 0.00408$, $F = 0.15$, $df = 70$, $p = 0.6954$). P values assess the null hypothesis that β , the overall population slope, is zero. A single regression line is shown when plots had a common slope; separate regressions indicate different random-effects slopes. Gray lines indicate a nonsignificant overall population slope.

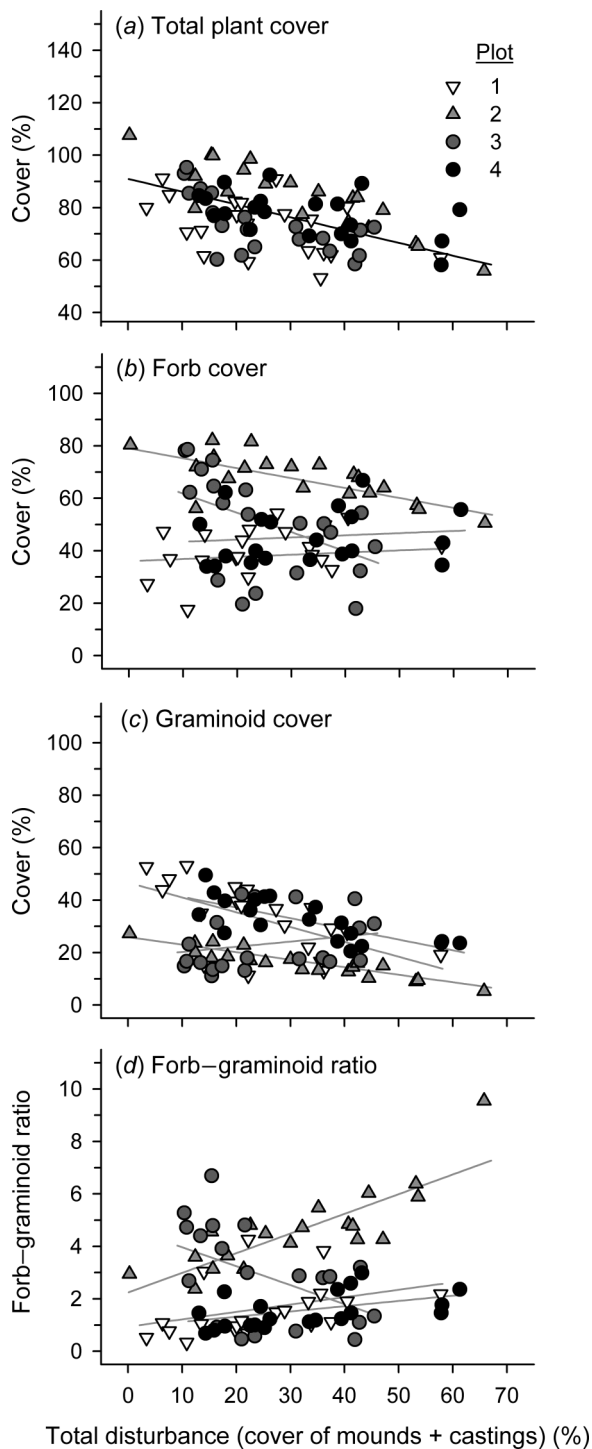
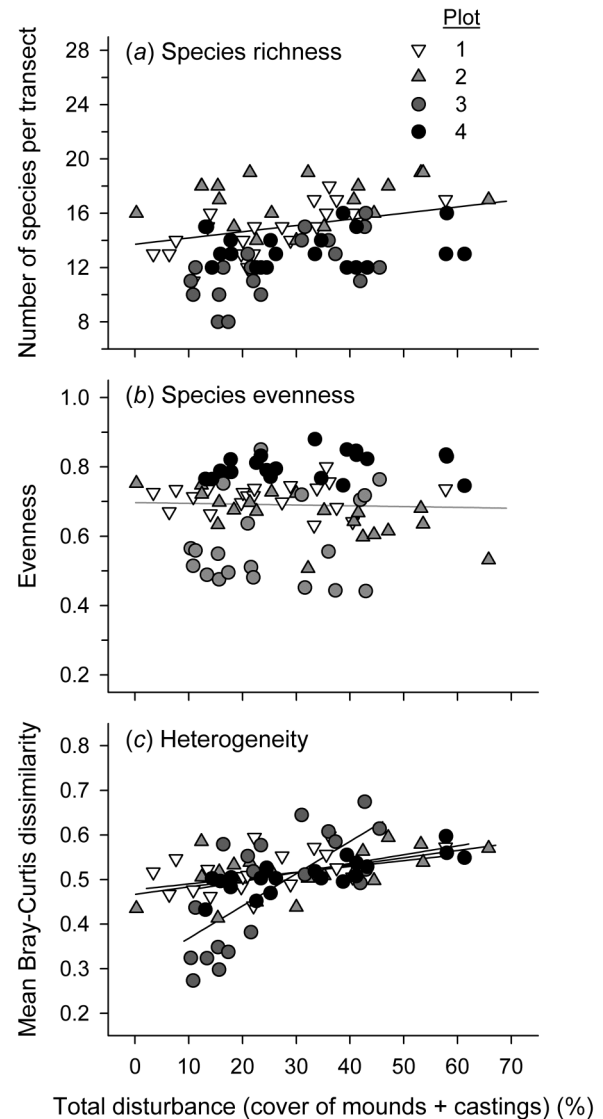


Fig. 3. Relationship between total disturbance (cover of mounds plus castings) and (a) species richness (number of species per transect) ($\beta = 0.04577$, $SE(\beta) = 0.01363$, $F = 11.27$, $df = 74$, $p = 0.0012$), (b) species evenness (modified Hill ratio) ($\beta = -0.00023$, $SE(\beta) = 0.00060$, $F = 0.147$, $df = 74$, $p = 0.7025$), and (c) heterogeneity (mean Bray-Curtis dissimilarity) ($\beta = 0.00304$, $SE(\beta) = 0.00153$, $d^2 = 8.5794 \times 10^{-6}$, $F = 4.01$, $df = 70$, $p = 0.0491$). P values assess the null hypothesis that β , the overall population slope, is zero. A single regression line is shown when plots had a common slope; separate regressions indicate different random-effects slopes. Gray lines indicate a nonsignificant overall population slope.



colonize gopher mounds by reemergence from burial or lateral growth (Umbanhowar 1995; Rogers and Hartnett 2001), in the montane meadows at Bunchgrass Ridge, the only graminoid to exhibit this trait was the rhizomatous sedge *Carex pensylvanica*. In contrast, the principal grass species had shallow fibrous roots and appeared to have colonized mounds by seed. Sherrod et al. (2005) observed a similar difference in the reemergence of graminoids and forbs in an alpine habitat. They attributed the greater recovery of forbs to greater carbohydrate reserves below ground; winter storage is advantageous when the growing season is short. Burial by castings, however, may not be sufficiently deep to differentially affect survival or emergence.

Table 2. Results of mixed-effects models of plant community responses to cover of old mounds and castings.

Community attribute	Model structure	Disturbance type	β	SE(β)	d^2	F	df	p
Total plant cover	I	Old mound	-0.4126	0.0913		23.33	73-77	<0.001
		Casting	-0.5902	0.1046		31.86	73-77	<0.001
Forb cover	I + S (C)	Old mound	0.0007	0.1039		0.000	69-77	0.9957
		Casting	-0.0978	0.5278	1.0437	0.034	69-77	0.8719
Graminoid cover	I + S (C)	Old mound	-0.4024	0.0751		37.87	69-77	<0.001
		Casting	-0.3572	0.3644	0.4947	0.927	69-77	0.3359
Forb-graminoid ratio	I + S (M + C)	Old mound	0.0517	0.0257	0.0022	9.60	65-77	0.0029
		Casting	0.0225	0.0518	0.0101	0.189	65-77	0.6651
Species richness	I	Old mound	0.0280	0.0187		2.81	73-77	0.0982
		Casting	0.0686	0.0214		10.33	73-77	0.0019
Evenness	I + S (M + C)	Old mound	-0.0036	0.0029	3.2×10^{-5}	1.22	65-77	0.2738
		Casting	0.0013	0.0019	1.3×10^{-5}	0.45	65-77	0.5045
Heterogeneity	I + S (M + C)	Old mound	0.0014	0.0006	2.1×10^{-9}	6.74	65-77	0.0116
		Casting	0.0037	0.0020	1.4×10^{-5}	2.03	65-77	0.1592

Note: Intercept-only (I) models have a common slope among plots for each fixed effect (cover of old mounds and castings). Intercept plus slope (I + S) models have different intercepts and slopes among plots, with different slopes for castings (C) or mounds and castings (M + C). The random slope variance (d^2) determines the by-plot variation about the overall population slope (β). For both model types, p values assess the null hypothesis that β is zero (significant slopes are in bold font).

A third, related distinction is that the mounds in this study were generally older than castings, deposited during previous growing seasons. Fresh mounds were virtually absent, possibly because most mounding occurs in late summer or fall (G.S. Olson, 2011, personal communication) or early-summer mounding was inhibited by the unusually late snowmelt in 2011. In contrast, castings were deposited just prior to plant emergence. It appears that the main effect of castings is to reduce or delay plant emergence indiscriminately and only in the current growing season, resulting in a rapid transition from a state of no plant cover to one in which both forbs and graminoids are present. In contrast, mounds revegetate more slowly (Jones et al. 2008), allowing sufficient time for differences in plant traits to be expressed. Longer-term observations, combined with burial experiments (e.g., Sherrod et al. 2005), would provide a more complete understanding of the timing and mechanisms of plant response to burial.

We also observed considerable variation in response to disturbance among plots (both within and among meadows), leading to our second question about the context dependency of these relationships. We speculate that much of this variation relates to species' compositional differences among plots. Although plots shared many species in common, their abundances often varied, and many forbs were found in only one plot (Table 1). Species within a growth form invariably differ in their susceptibility to burial and rates of regrowth, reflecting differences in storage organs (e.g., tuber, caudex, or rhizome) or methods of perennation (Antos and Zobel 1985). Indeed, the slopes of species cover-disturbance relationships varied markedly among taxa (M.F. Case, unpublished data). As a consequence, the summed responses of these broadly defined groupings (forbs and graminoids) can be sensitive to the traits of the local species pool. As composition changes, so do relationships with disturbance.

Diversity and heterogeneity

We hypothesized that transect-scale richness would decline or, alternatively, display a hump-shaped pattern with disturbance. A decline would be consistent with observations of increasing richness on mounds as they age (Rogers et al. 2001; Sherrod et al. 2005; Jones et al. 2008). In contrast, a hump-shaped (IDH) pattern would suggest presence of competitive or ruderal species at opposite ends of the disturbance gradient and their coexistence at intermediate levels of disturbance (Connell 1978). Richness conformed to neither of these patterns; instead, it was positively correlated with disturbance. In contrast, trends in species evenness and heterogeneity (variation in species composition) did conform to expectation: evenness showed no relationship with disturbance and heterogeneity was positively correlated (a pattern driven by

mounds). These results are consistent with those of Jones et al. (2008), who demonstrated greater heterogeneity of species composition among mounds than among similar-sized patches of undisturbed meadow.

In combination, these results provide a clear illustration of how diversity-disturbance relationships can vary with the scale of observation (Auerbach and Shmida 1987; Chaneton and Facelli 1991). Transects represent the aggregation of many disturbed and undisturbed patches (quadrats). Although small disturbed patches contain fewer species, on average, than undisturbed patches do, they are more heterogeneous — more likely to contain species that are unique to a patch (Jones et al. 2008). The local density of species along a transect is reduced by disturbance, yet the potential for rarer species to establish is increased. Conversely, high levels of disturbance (as large as 60% cover among transects) do not appear to eliminate species from a transect; if species were lost, we would expect either no relationship with disturbance (if gains were balanced by losses) or a hump-shaped (IDH) pattern (if losses outweighed gains). A hump-shaped pattern is still theoretically possible (with few species present at very high disturbance). Yet, it is unlikely that our inability to demonstrate this pattern reflects an incomplete sample of the disturbance gradient (e.g., Sousa 1984), as plots were chosen such that transects would encompass the full range of ground disturbance in these meadows.

Conclusions

Gopher disturbances are prominent and ecologically important features of these high-elevation meadows. By considering responses to castings and patterns at spatial scales considerably larger than individual mounds, our study yields new insights into the contributions of gopher disturbance to plant community structure. Castings reduce plant cover, but effects are transient and nonselective compared with mounds, which are larger, denser, and more persistent. Even so, variation among meadows in the correlations between disturbance and growth-form abundance suggests that the nature or strength of these relationships can vary with the composition and regenerative traits of the local species. Finally, gopher disturbances reduce species richness locally, but enhance diversity and heterogeneity at larger spatial scales. The combination of frequent, small-scale disturbance and a flora that is largely resilient to burial results in a shifting mosaic of vegetation states in time and space.

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